Behavioral Stochastic Resonance within the Human Brain

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We provide the first evidence that stochastic resonance within the human brain can enhance behavioral responses to weak sensory inputs. We asked subjects to adjust handgrip force to a slowly changing, subthreshold gray level signal presented to their right eye. Behavioral responses were optimized by presenting randomly changing gray levels separately to the left eye. The results indicate that observed behavioral stochastic resonance was mediated by neural activity within the human brain where the information from both eyes converges.

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The brain is a noisy processor where robust output responses, particularly to weak inputs, are not guaranteed. However, in some cases, noise can play a constructive role in information transfer via a mechanism known as stochastic resonance (SR), whereby the response of a nonlinear system to a weak input signal is optimized by the presence of a nonzero level of noise [1].

Studies of SR in neurobiological information transfer have evolved from the level of single sensory receptors [2] to that of neuronal networks within the central nervous system [3], targeting constructive roles of noise in information processing in the brain. Because these neurobiological studies do not deal directly with functional aspects of SR, more recent studies have focused on the noise-induced improvement in behavioral and/or functional performance in animals [4] and humans [5]. Behavioral SR studies so far, however, have adopted a single receptor design in which both noise and signal are injected into the same receptor. Thus, the interaction site is again the sensory periphery, not the central brain.

To study SR in the brain, Hidaka *et al.* [6] and Mori and Kai [7] used a double receptor design, where noise and signals are injected into two distinct receptors from which neuronal inputs first converge more centrally within the brain. Nonetheless, these studies observed only noise-enhanced responses in human autonomic outflows relevant to falling blood pressure [6] and in human brain waves to a periodic visual input [7], not behavioral consequences of SR.

In this Letter, we describe an experiment that used the double receptor design to demonstrate the behavioral consequences of SR occurring within the human brain.

We investigated human subjects' responses, in a sensorimotor integration task, to the slowly changing gray level of an image presented on a computer screen. An important feature of our experiment is that different visual stimuli were separately presented to both eyes using a mirror stereoscope [Fig. 1(a)]; we injected the visual stimulus to the right eye as a signal and investigated how the behavioral response to the weak signal, quantified by handgrip force, would be affected by presenting random visual stimuli to the left eye [8]. Neural inputs from both eyes first converge in the primary visual cortex and are integrated via binocular interaction higher in the visual system [7]. Therefore, when signal and noise were presented to separate eyes, changes in sensorimotor integration, if any, would take place not at the peripheral level but rather at some higher visual centers.

All 19 subjects (21–32 years) had normal or corrected-to-normal visual acuity. The stimulus signals presented at the right eye window consisted of single sinusoids (baseline gray level = 100, luminance 16.6 cd m^{-2}) and interval periods (gray level = 100). Frame rates of the signal and noise were set to 10 Hz. Cycle lengths of the sinusoidal part were randomly assigned to 3, 4, or 5 sec, but they were held constant throughout each trial. To prevent the subjects' prediction of the phase of the stimulus signal, the duration of each intercycle interval period was randomly set within the cycle length of the sinusoid.

To quantify the subjects' responses, we used Stevens's classical psychophysical technique of cross-modality matching [9] wherein subjects match the proprioceptive sensation of muscular force to visual perception of brightness; we asked subjects to adjust their handgrip force to the time-varying gray level of the image [10]. Because the signal amplitude was tuned to be weak and subthreshold without noise, the subject generated an output handgrip force that contained some high- and/or low-frequency components [F, Fig. 1(b)]. Thus, the visual stimulus and handgrip force signals were filtered by convolving them with a single sinusoid [$\sin(-2\pi t/T)$ only when $0 \le t \le T$] whose cycle length was the same as that of the stimulus signal. Then, lag-zero cross-correlation coefficients were calculated between these two filtered time series.

To obtain probability distributions for the cross-correlation coefficient and the variance of phase

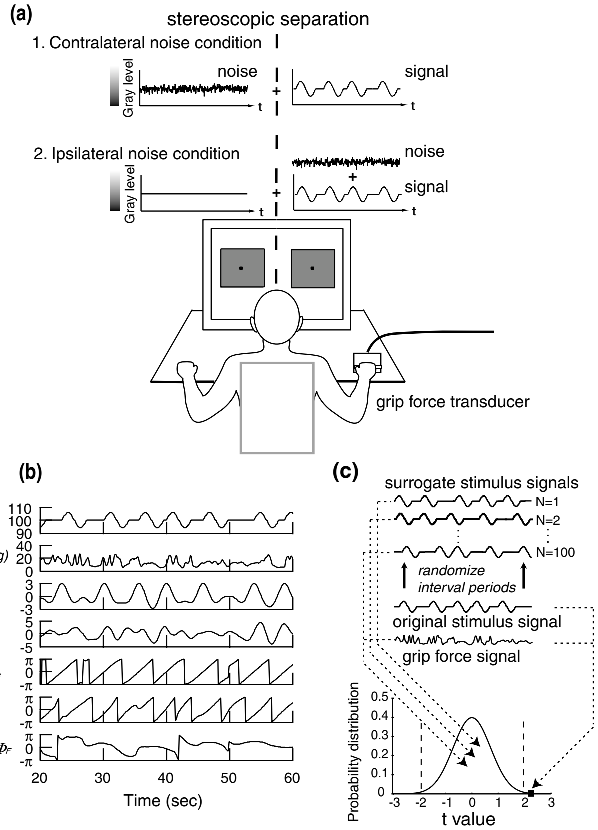

FIG. 1. (a) Experimental setup. Subjects adjusted handgrip force to the slowly changing gray level of the right eye window, while Gaussian white noise was added to the left eye window (contralateral noise) or to the right eye window (ipsilateral noise). (b) Representative recording from one subject in the contralateral noise condition (subject B in Fig. 2; subthreshold signal amplitude $= 6$, and noise SD $= 4$). G: visual stimulus signal; F: handgrip force; $\hat{G}$: filtered visual stimulus signal; $\hat{F}$: filtered handgrip force signal; ϕ_G: instantaneous phase of $\hat{G}$; ϕ_F: instantaneous phase of $\hat{F}$; and ϕ_F-ϕ_G: phase differences between ϕ_F and ϕ_G. (c) One hundred sets of surrogate signals were generated by randomly modifying the interval lengths of the original visual signal. The t values for correlation/synchronization measures of the original data were calculated from the probability distribution obtained from these surrogates.

differences (see below) to test statistically the null hypothesis that subjects' behavior was not driven by the visual stimulus, we generated 100 sets of surrogate data where the interval periods of the original signal were randomly modified. The t value of the actual data was used for the statistical test [Fig. 1(c)]. We confirmed that the distribution was not significantly different from the Gaussian distribution before calculating t values.

We first determined a signal amplitude that the subject was unable to perceive by presenting the signal to his/her right eye alone. We started from the amplitude of a single sinusoidal gray level signal of 32 (mean $= 100$) and successively reduced it by one-half until a nonsignificant t value ($t < 1.98$ for $p > 0.05$) for the lag-zero cross-correlation coefficient between the input and output signals, calculated by using 100 surrogate data sets, was observed [Fig. 1(c)]. Then, the amplitude was finely tuned by successively adding 1 as long as the t value continued to be less than 1.98. We regarded a signal amplitude as being subthreshold when t values smaller than 1.98 were observed 3 times in succession at that amplitude. This amplitude (6.2 ± 3.0, mean $\pm$ SD over all subjects) was used throughout the following noise test session. At the end of the experiment, we confirmed again that this amplitude was still subthreshold.

In the noise test session, Gaussian white noise with zero mean and standard deviation (SD) of 2, 4, 6, 8, 12, or 20 was added to the subthreshold gray level signal presented to the right eye [ipsilateral noise, Fig. 1(a)], or to the constant gray level (100) of the image presented to the left eye [contralateral noise, Fig. 1(a)] on each frame. The presentation order of the different noise levels was randomized.

The effect of noise intensity on cross-correlation coefficients for three subjects is shown in Figs. 2(a), 2(c), and 2(e). In subjects A and B, cross-correlation coefficients, which were almost zero without noise, were maximized at intermediate noise levels. They declined again to almost zero at higher noise levels both for contralateral and ipsilateral noise. As indicated by the t values, improvements at intermediate levels of noise were statistically significant ($t > 1.98$ for $p < 0.05$) in subjects A and B [Figs. 2(a) and 2(c)]. The positive effect of noise was sometimes ambiguous, however, a significant t value was observed only at one (ipsilateral) noise level in subject C [Fig. 2(e)]. In total, significant t values were observed at some nonzero noise levels in 12 of 19 subjects both for ipsilateral and contralateral noise. Seven subjects exhibited significant t values in both noise conditions. These results indicate that the addition of visual noise often can allow a subthreshold visual stimulus to drive behavior in both contralateral and ipsilateral noise conditions.

Because the cross-correlation measure could be sensitive to trends and/or sudden increases or decreases in handgrip force, we further examined whether the subjects could synchronize their behavior with the weak input signals by calculating the nonlinear instantaneous phase difference [11] between visual signals and handgrip force [Fig. 1(b)].

The instantaneous phase of the filtered signal was obtained via construction of an analytic signal. The analytic signal $\zeta(t)$ of an arbitrary signal $f(t)$ can be calculated as

$$\zeta(t) = f(t) + j\tilde{f}(t) = A(t)e^{j\phi(t)}, \quad (1)$$

where the function $\tilde{f}(t)$ is the Hilbert transform of $f(t)$,

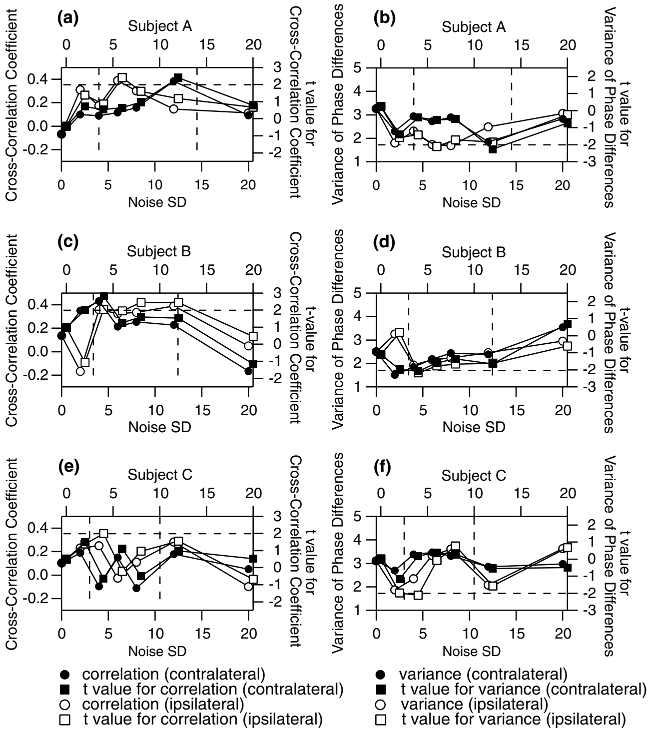

FIG. 2. Effects of noise intensity on cross-correlation coefficients and variance of phase differences for three subjects (A, B, C). Two vertical lines in each graph indicate the normalized noise level where noise SD/signal amplitude = 0.5 (left line) and 2.0 (right line).

$$\tilde{f}(t) = \pi^{-1}\text{P.V.}\int_{-\infty}^{\infty} \frac{f(\tau)}{t-\tau}d\tau, \quad (2)$$

and P.V. means that the integral is taken in the sense of Cauchy principal value. The instantaneous amplitude $A(t)$ and the instantaneous phase $\phi(t)$ of $f(t)$ are thus uniquely obtained from Eq. (1). [However, $A(t)$ was not used in this study.]

To quantify the phase difference between visual stimulus and handgrip force signals, the variance of phase differences V was calculated as

$$V = \sum_{t=1}^{N}[\{\phi_G(t) - \phi_F(t)\} - \frac{1}{N}\sum_{t=1}^{N}\{\phi_G(t) - \phi_F(t)\}]^2, \quad (3)$$

where $\phi_G(t)$ and $\phi_F(t)$ are, respectively, the instantaneous phases of visual stimulus and handgrip force signals, and N is the number of data points ($N = 700$).

Figures 2(b), 2(d), and 2(f) demonstrate typical examples for the variance of phase differences and their t values. In subjects A and B, the variance of phase differences decreased at intermediate noise levels in both noise conditions, indicating that the phase between visual signal and handgrip force was more synchronized; this enhanced phase synchronization was significant ($t > 1.98$ for $p < 0.05$). In subject C, the significant improvement in phase synchronization was observed only for ipsilateral noise [Fig. 2(f)]. For variance of phase differences, 10 of 19 and 13 of 19 subjects demonstrated significant t values at some nonzero noise levels for contralateral and ipsilateral noise, respectively. Therefore, behavioral SR was confirmed from the viewpoint of phase synchronization.

The noise levels where significant improvement in behavioral driving by the subthreshold signal was observed varied considerably among subjects. Nonetheless, these optimal noise levels normalized by the subthreshold signal amplitude for each subject mostly fell in the range of $0.5 < \text{SD/amplitude} \leq 2.0$ in both contralateral and ipsilateral noise conditions (Fig. 2). Thus, we categorized the noise SD into four levels, i.e., without noise ($\text{SD} = 0$), weak noise ($0 < \text{SD/amplitude} \leq 0.5$), intermediate noise ($0.5 < \text{SD/amplitude} \leq 2.0$), and intense noise ($\text{SD/amplitude} > 2.0$), and compared the group means across the categorized noise levels for behavioral driving by the subthreshold signal, both for the cross-correlation coefficient and for the variance of phase differences.

A significant difference across the categorized noise levels was observed for both measures of behavioral driving by the subthreshold signal (Fig. 3) (two-way ANOVA, noise levels × subjects) in both contralateral [cross-correlation coefficient: $F(3, 54) = 4.11$ ($p < 0.01$); variance of phase differences: $F(3, 54) = 3.34$ ($p < 0.05$)] and ipsilateral [cross-correlation coefficient: $F(3, 54) = 2.85$ ($p < 0.05$); variance of phase differences: $F(3, 54) = 5.66$ ($p < 0.005$)] noise conditions. A *post hoc* analysis using the Dunnett test exhibited significant differences between "without noise" and "intermediate noise" in both contralateral and ipsilateral noise conditions ($p < 0.05$). These results indicate that the behavioral driving by subthreshold signals can be improved by adding noise with an SD ranging from a half to twice that of the signal amplitude to either the contralateral or the ipsilateral eye.

The uniqueness of our study lies in the demonstration of noise-enhanced sensorimotor integration in the human cortices, which could not be shown by previous single receptor SR studies [5]. Also, it improves on a recent behavioral SR study by Usher and Feingold [12], demonstrating auditory noise-enhanced performance of a visually imposed arithmetic multiplication task, in that the site of interaction between noise and signal can be located at the cortical areas relevant for sensorimotor integration. Indeed, a recent study by Rodriguez *et al.* [13] has shown a long-distance pattern of synchronization in electrical brain activity between visual and motor cortical areas when the cognition of ambiguous visual stimuli triggers the motor response. This and the fact that added noise can enhance synchronization among many coupled oscillators [14] would lead to a testable hypothesis that the noise-enhanced sensorimotor integration we observed in the

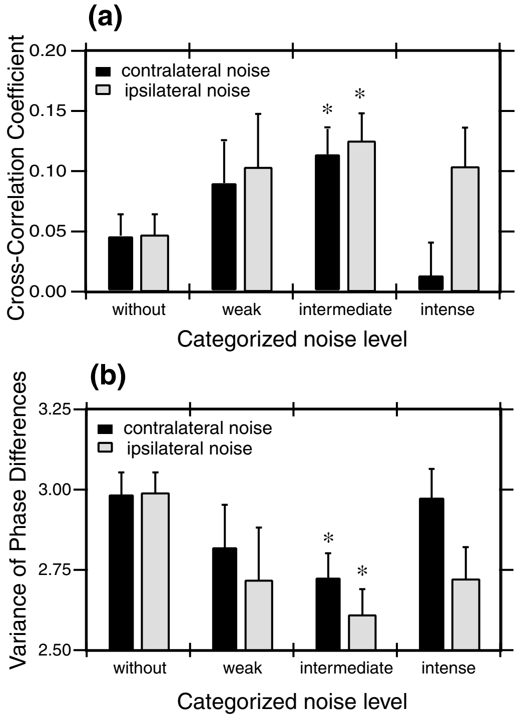

FIG. 3. Effects of normalized and categorized noise levels on cross-correlation coefficients (a), and variance of phase differences (b). Black and gray bars, respectively, represent group means for contralateral and ipsilateral noise at each noise level; without noise (SD = 0), weak ($0 < \mathrm{SD/amplitude} \leq 0.5$), intermediate ($0.5 < \mathrm{SD/amplitude} \leq 2.0$), and intense ($\mathrm{SD/amplitude} > 2.0$) noise. Error bars correspond to the standard error of the mean $*$; significant difference between "without noise" and "intermediate noise level" ($p < 0.05$).

contralateral condition might be associated with an increased synchrony of the neural activity of sensorimotor areas.

Mechanisms of binocular information processing concerning brightness, especially for the temporally dynamic case, remain unclear [15]. The results of the present study suggest the existence of dynamic binocular interaction in the human brain and may help us understand how the brain combines and processes luminance information from our two eyes. In addition, the concept of noise-enhanced sensorimotor integration within the human brain might also be useful in designing some optical human interfaces that could help us respond to weak visual inputs, e.g., while driving a vehicle in twilight.

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[8] Images for both eyes were presented in the dark at two rectangular windows (200×190 pixels) on a CRT monitor (640×480 resolution; 154 Hz refresh rate) controlled by a Macintosh computer [Fig. 1(a)]. A black square (10×10 pixels) at the center of each window served as a fixation target. Each image window was presented separately to each eye using a mirror stereoscope (TKK 129, Takei Scientific Instrument) at a distance of 45 cm from the monitor. The background gray levels (0–255, luminance 0.03–149.8 $\mathrm{cd\,m^{-2}}$) around the fixation targets of the two windows were spatially uniform and served as temporally changing visual stimuli.

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